

## Characteristic High- and Low-Frequency Dental Traits in Sub-Saharan African Populations

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**ABSTRACT** In an earlier investigation (Irish [1993] *Biological Affinities of Late Pleistocene Through Modern African Aboriginal Populations: The Dental Evidence* [Ann Arbor: University Microfilms]), biological affinities of 32 sub-Saharan and North African dental samples were estimated using comparative analyses of 36 dental morphological traits. Marked dental homogeneity was revealed among samples within each of the two geographic regions, but significant interregional differences were noted. Assuming dental phenetic expression approximates or is an estimate of genetic variation, the present study of 976 sub-Saharan-affiliated Africans indicates they are not closely related to other world groups; they are characterized by numerous morphologically complex crown and root traits. Turner ([1984] *Acta Anthropogenetica* 8:23-78; [1985] in R Kirk and E Szathmary (eds.): *Out of Asia: Peopling the Americas and the Pacific* [Canberra: The Journal of Pacific History], pp. 31-78; [1990] *Am. J. Phys. Anthropol.* 82:295-318; [1992] *Persp. Hum. Biol. 2/Archaeol. Oceania* 27:120-127; [1992] in T Akaszawa, K Aoki, and T Kimura (eds.): *The Evolution and Dispersal of Modern Humans in Asia* [Tokyo: Hokusen-Sha Publishing Co.], pp. 415-438) reports that Northeast Asian/New World sinodonts also have complex teeth relative to Europeans, Southeast Asian sundadonts, Australian/Tasmanians, and Melanesians. However, sinodonty is characterized by UI1 winging, UI1 shoveling, UI1 double shoveling, one-rooted UP1, UM1 enamel extension, M3 agenesis, and three-rooted LM1. Sub-Saharan peoples exhibit very low frequencies of these features.

It is proposed that the collection of dental traits which best differentiate sub-Saharan Africans from other worldwide samples includes high frequencies of the Bushman Canine, two-rooted UP1, UM1 Carabelli's trait, three-rooted UM2, LM2 Y-groove pattern, LM1 cusp 7, LP1 Tome's root, two-rooted LM2, UM3 presence, and very low incidences of UI1 double shoveling and UM1 enamel extension. This suite of diagnostic traits is termed the sub-Saharan African dental complex. *Am J Phys Anthropol* 102:455-467, 1997.

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With respect to the search for hominid origins, more intensive physical anthropological inquiry has centered on Africa than any other region of the world. By comparison, little has been done concerning the physical anthropology of recent African native populations and their origins and affinities. For the most part, what has been accomplished involves anthropometric, os-

teological, and genetic analyses. Several studies are quite thorough (e.g., among oth-

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ers, Oschinsky, 1954; DeVilliers, 1968; Tobias, 1966, 1974, 1985; Hiernaux, 1975; Nurse et al., 1985; Lundy, 1986, Excoffier et al., 1987); however, most are narrow in scope, addressing only specific regions and tribes. These shortcomings are exacerbated in the field of dental anthropology which, with few notable exceptions (e.g., Shaw, 1931; Greene, 1967, 1972; Jacobson, 1982; Hassanali and Mwaniki, 1984; Sakuma and Ogata, 1987; Turner and Markowitz, 1990), has been largely ignored in the study of African peoples. Moreover, like most African physical anthropological investigations, the dental studies commonly involve a limited number of traits and samples; in only a few instances (e.g., Greene, 1982; Irish and Turner, 1990) do any attempt comparisons between groups and/or regions.

Recently, I addressed the general paucity of African physical anthropological data and the specific lack of comprehensive dental study through a diachronic analysis of dental traits in samples throughout the continent (see Irish, 1993). The present paper reexamines three aspects of this larger study, with special attention paid to sub-Saharan peoples. First, the samples, dental traits, and methodologies employed are reviewed. Second, dental data observed in the sub-Saharan African-affiliated samples are compared to those of North Africans. The results help to characterize the peoples of this vast continent and assess their dental affinities to one another. Third, the data are contrasted with published findings from several non-African groups to give an initial, global perspective of African affinities and identify those traits which best distinguish sub-Saharan peoples from other world populations.

## MATERIALS AND METHODS

Thirty-two late prehistoric, historic, and modern sub-Saharan and North African human samples (Table 1) were analyzed in the original dental morphological study (Irish, 1993); all but one, Mesolithic Nubia, were recorded by the author. For the present study, 31 samples are examined further, and the Mesolithic Nubian sample, originally scored by C.G. Turner II, was rescored to

negate potential interobserver error. Twenty-eight of these samples represent specific African cultures (Fig. 1) based on their recorded and researched tribal and/or linguistic affiliations. The remaining four represent pooled samples of individuals from the same broad geographic regions (i.e., west, east, south, and north Africa).

The 32 samples (1,635 total dentitions) are a representative cross-section of native African cultural groups and include all of Greenberg's (1959, 1966) African language superfamilies: Afroasiatic, Nilo-Saharan, Congo-Kordofanian, and Khoisan. Thirty samples consist of well-preserved skeletal dentitions; the other two consist either entirely (Sotho [ $n = 178$ ]) or partly (San [83 of 99]) of dental hard stone casts taken of living individuals (Morris, personal communication; Haeussler et al., 1989). Thirty-six dental and osseous morphological traits from the maxilla and mandible were observed in those samples with skeletal dentitions (Table 2). Only 28 traits were recorded in the Sotho because root traits, UM1 enamel extension, and rocker jaw cannot be depicted in casts.

Except for UI1 midline diastema (see Van Reenen, 1964), all traits used in the present study are included in the ASU Dental Anthropology System. Procedures used in the ASU system are based on well-established criteria for scoring intratrait variation (for a complete discussion see Turner et al., 1991). The traits in each individual were recorded with the aid of 23 ASU and Dahlberg Zoller Laboratory rank-scale reference plaques. Only the specimen's highest antimere expressions were analyzed for each trait; this maximizes the genetic potential for these polygenic features (Turner et al., 1991). Previous studies indicate that few significant dental morphological differences exist between males and females (Scott, 1973, 1980; Smith and Shegev, 1988; Bermudez de Castro, 1989; Turner et al., 1991; Hanihara, 1992). As such, it is standard procedure to pool the sexes when employing the ASU system (Turner, unpublished; Turner et al., 1991).

A lack of sexual dimorphism is supported by the present study. Pearson chi-square analysis of the combined samples found that only the UP1 root number, UM2 root num-

TABLE 1. The 32 African dental samples (modified from Irish, 1993)

Sample name	Country	Culture/tribal affiliation	Period	No.	Sample location	
Sub-Saharan Africa						
Congo	Congo	Teke, Kongo	19th century	30	AMNH, MH <sup>1</sup>	
Gabon	Gabon	Fang, Nkomi, Lumbo, Mpongwe	19–20th century	39	MH, NMNH	
Ghana	Ghana	Ashanti, Fanti	19th century	47	AMNH	
Kenya	Kenya, Tanzania	Kikuyu, Swahili, Chaga, Pare	19–20th century	114	AMNH, MH, NMNH	
Khoikhoi	South Africa	Nama, Korana, and unspecified	19th century	37	AMNH, MH	
Nguni	South Africa	Zulu, Xhosa	19th century	22	AMNH, NMNH	
Nigeria/Cameroon	Nigeria, Cameroon	Efik, Ibibio?, Boki, Anyang	19th century	57	AMNH	
Pygmy	Congo, Gabon	Binga, Bongo	19–20th century	22	AMNH, MH	
San	Botswana, South Africa	!Kung, Naron, Tshakwe, Mkaukau	Modern	99	AMNH, ASU	
Senegambia	Senegambia	Wolof, Balante, Serer	19–20th century	43	MH, NMNH	
Sotho	South Africa	Pedi	Modern	178	ASU	
Tanzania	Tanzania, Zanzibar	Nyamwezi, Ngindo, Hehe, Gogo	19–20th century	44	AMNH, MH	
Togo/Benin	Togo, Benin	Ewe, Fon	19th century	25	AMNH	
Tukulor	Senegambia	Tukulor	19–20th century	39	MH	
North Africa						
Algeria	Algeria	Berber	19th century	26	MH	
Bedouin	Morocco, Tunisia, Libya	Arab	19–20th century	49	MH, UM	
Canary Islands	Canary Islands	Guanche	AD 400–900?	163	AMNH, MH, NMNH	
Carthage	Tunisia	Phoenician	751–146 BC	28	MH	
Chad	Chad	Toubou, Masalit, Kanembu	19–20th century	29	MH	
Christian	Sudan	Christian Period	AD 550–1350	18	ASU	
El Hesa	Egypt	Egyptian	AD 200–400	72	AMNH	
Kabyle	Algeria	Berber	19–20th century	32	MH	
Kharga	Egypt	Egyptian	AD 500–600	26	NMNH	
Lisht	Egypt	Egyptian	1991–1783 BC	61	NMNH	
Meroitic	Sudan	Meroitic Period	100 BC–AD 350	91	ASU	
Mesolithic	Sudan	Nubians	Mesolithic Period	10000–12000 BC	67	SMU
Soleb	Sudan	Nubians	New Kingdom Period	1575–1380 BC	32	MH
X-Group	Sudan	Nubians	X-Group Period	AD 350–550	39	ASU
Regional African samples						
North Africa	Algeria, Chad	Capsian, Mdaga, Bou-douma	Prehistoric/modern	22	MH, UM	
West Africa	Cameroon, Ghana, Liberia, etc.	Mabeya, Mandingo, Sanga, Golah	Prehistoric/historic	49	AMNH, MH	
East Africa	Zimbabwe, Ruanda, Kenya, etc.	Masai, Nuer, ?	19–20th century	26	AMNH, MH, NMNH	
South Africa	Namibia, Zaire, South Africa	?	19th century	9	AMNH, MH, NMNH	

<sup>1</sup> AMNH, American Museum of Natural History; ASU, Arizona State University; MH, Musée de l'Homme de Paris; NMNH, National Museum of Natural History; SMU, Southern Methodist University; UM, University of Minnesota.

ber, and UM3 congenital absence traits differ significantly ( $P \leq .05$ , 1 df) between sexes; females display higher frequencies of root fusion and UM3 agenesis. However, any potential bias which may result from the use of these three traits should be largely offset by comparable sex ratios in both individual

and pooled samples (e.g., males = 46%, females = 40%, and ? = 14% of 1,635 individuals). Therefore, the sexes are pooled for all analyses in order to include these important traits yet maximize sample sizes.

Following recordation, trait frequencies were determined for the 32 samples, and

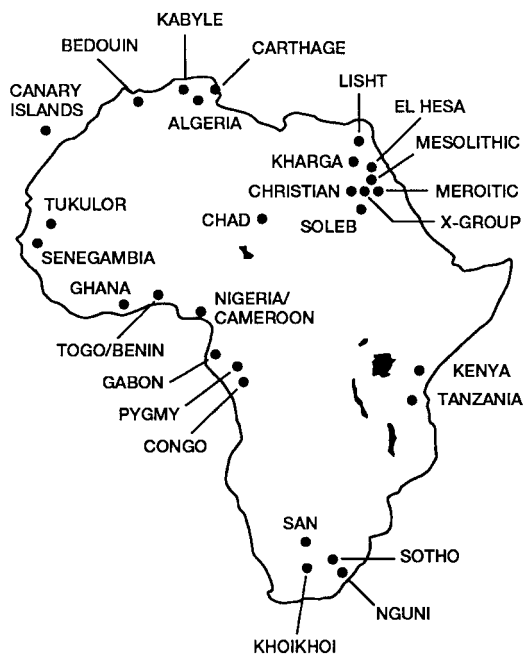


Fig. 1. Origin locations of the North African and sub-Saharan African samples.

TABLE 2. The 36 dental and osseous traits<sup>1</sup> used in the study

Maxilla	Mandible
Winging UI1	Lingual cusp number LP2
Labial curvature UI1	Anterior fovea LM1
Palatine torus	Mandibular torus
Shovel UI1	Groove pattern LM2
Double shovel UI1	Rocker jaw
Midline diastema UI1 <sup>2</sup>	Cusp number LM1
Interruption groove UI2	Cusp number LM2
Tuberculum dentale UI2	Deflecting wrinkle LM1
Bushman Canine UC	Distal trigonid crest LM1
Distal accessory ridge UC	Protostylid LM1
Hypocone UM2	Cusp 7 (metaconulid) LM1
Cusp 5 (metaconule) UM1	Tome's root LP1
Carabelli's trait UM1	Root number LC
Parastyle UM3	Root number LM1
Enamel extension UM1	Root number LM2
Root number UP1	Torsomolar angle LM3
Root number UM2	
Peg-reduced UI2	
Odontome P1-P2	
Congenital absence UM3	

<sup>1</sup> Traits from ASU dental anthropology system (Turner et al., 1991).

<sup>2</sup> Trait not used in ASU system.

C.A.B. Smith's Mean Measure of Divergence (MMD) statistic, using the Freeman and Tukey angular transformation (Berry and Berry, 1967; Sjøvold, 1973, 1977; Green and Suchey, 1976), was employed on the 28

samples of known cultural affiliation. This multivariate technique provides a quantitative estimate of biological divergence between samples, based on the degree of phenetic similarity (e.g., Sokal and Sneath, 1963) of dental traits. A lower MMD value indicates greater similarity and vice versa. It is assumed that phenetic similarity approximates cladistic relationship (Sokal and Sneath, 1963; Scott et al., 1983).

Twenty-seven samples were compared on the basis of all 36 traits. However, as noted, the Sotho sample can be analyzed using only 28 traits. Thus, to determine if comparisons based on the different numbers of traits affect the numerically derived MMD affinities, all 28 samples were also analyzed using just the 28 Sotho traits. Changes in the magnitudes of MMD values between samples in the 36 and 28 trait comparisons are negligible ( $r = .92$ ). Therefore, despite being characterized by fewer traits, the Sotho relationship to other samples is felt to represent an adequate dental classification (see below).

Lastly, the trait frequencies were compared to data recorded by C.G. Turner (1985, 1987, 1992a,b) in dental samples from Europe, Southeast Asia, Northeast Asia and the New World, Melanesia, and Australia/Tasmania to 1) learn how sub-Saharan Africans differ and 2) identify those traits which are most characteristic, relative to other world populations. The African/non-African comparisons also involved descriptive and MMD techniques. In addition, Pearson chi-square analysis was used to determine which individual traits differ significantly between samples.

## RESULTS AND DISCUSSION

### African sample comparisons

The 36 trait MMD results reveal a significant divergence between most sub-Saharan and North African samples but measurable sample homogeneity within the regions, particularly North Africa. A substantial table of these MMD values among all 28 samples is presented in Irish (1993) and is not included in this brief paper.<sup>1</sup> Instead, the dental phenetic relationships are visualized in a plot of MMD values among samples (Fig. 2)

<sup>1</sup>The MMD table is also available upon request.

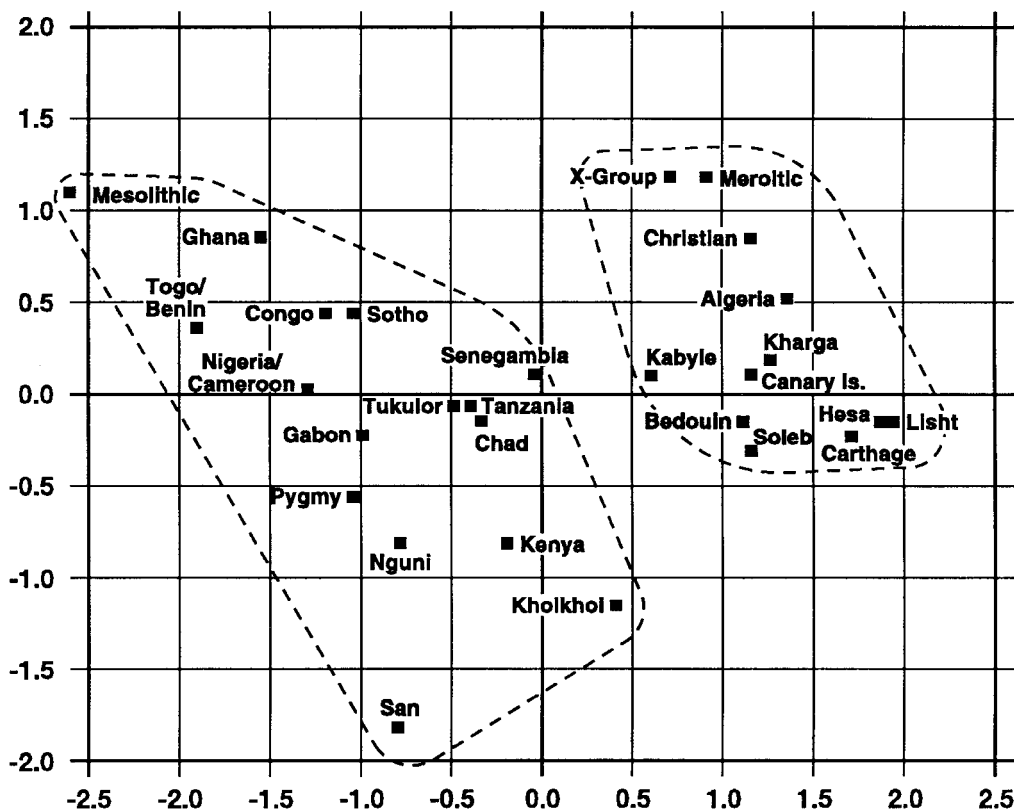


Fig. 2. Multidimensional scaling of MMD values among the 28 African samples based on the 36 dental traits.

using multidimensional scaling (MDS) (Kruskal and Wish, 1978).

Figure 2 shows that the 14 sub-Saharan samples, plus Mesolithic Nubia and Chad, group together on the left, suggesting much dental trait similitude. The Chad and Mesolithic Nubia samples exhibit many mass-additive dental traits consistent with a sub-Saharan affinity; this is the reason for their relative locations on the MDS configuration (for a detailed discussion see Irish and Turner, 1990; Irish, 1993). The average MMD value among the 16 samples is 0.051 (sum of all pairwise MMD comparison values divided by the total number of comparisons). The remaining North African samples are plotted in a tighter grouping on the right. Their corresponding average MMD is only 0.019, which suggests greater intraregion dental homogeneity. Finally, an obvious dichotomy is apparent between the sub-Sa-

haran and North African MDS groupings. The much higher average MMD value between samples from these two regions is 0.125. This regional separation is more clearly illustrated using cluster analysis (e.g., Aldenderfer and Blashfield, 1984; Everitt, 1980; Romesburg, 1984). Figure 3 presents the results of Ward's hierarchical agglomerative cluster analysis on the MMD values; the North Africans cluster at the top of the dendrogram, and the sub-Saharan-affiliated samples cluster at the bottom. Analogous results were obtained using single and complete linkage methods, implying internal consistency or stability of the MDS and cluster solutions (Aldenderfer and Blashfield, 1984). Moreover, the differing levels of intraregion homogeneity are also nicely depicted, although some aspects of specific clusters (e.g., Pygmy-Tukulor-Khoikhol) represent an artifact of the clustering algorithm

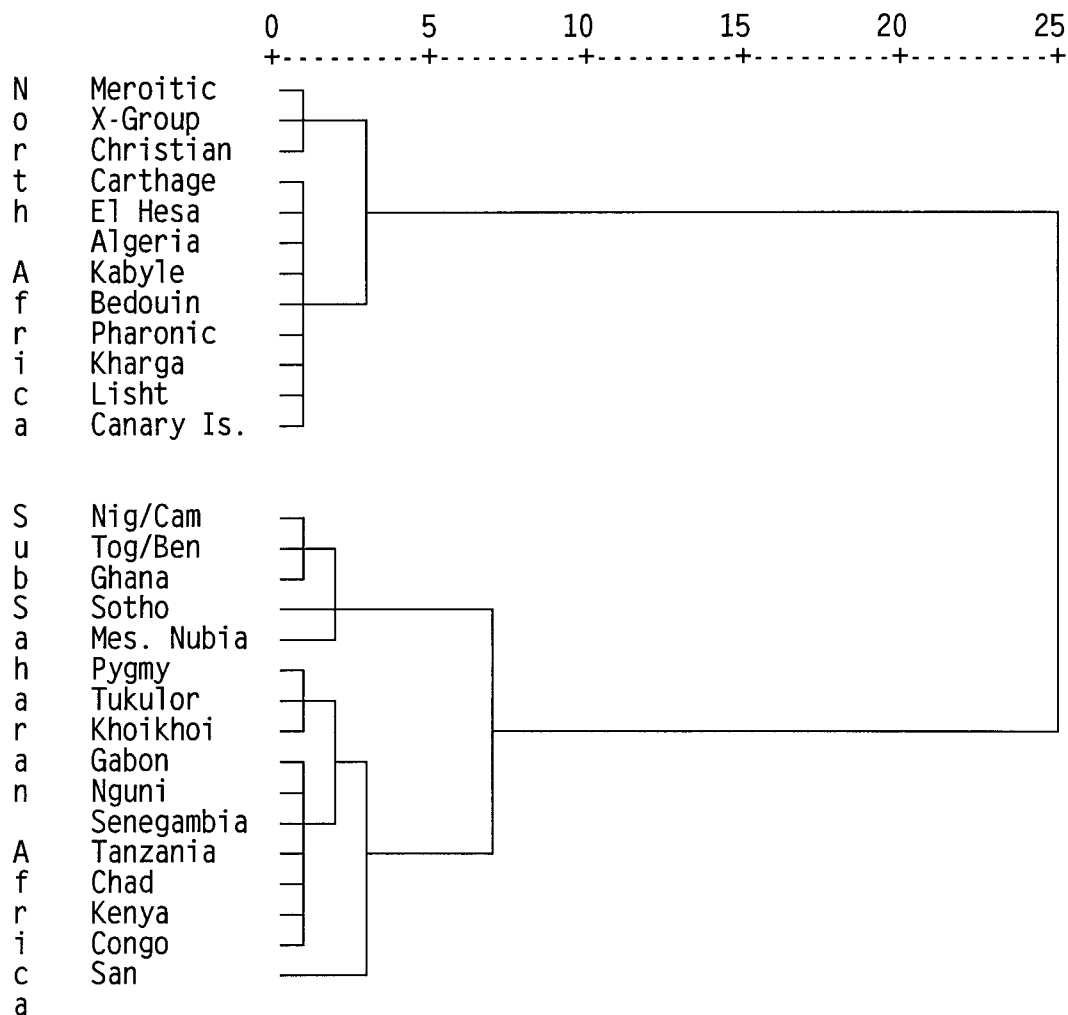


Fig. 3. Ward's method cluster dendrogram of MMD values among 28 African samples based on 36 dental traits.

rather than actual affinities (compare to MDS).

These dental-based affinities reflect those using genetic, skeletal, dermatoglyphic, anthropometric, linguistic, and cultural data (see among others, Mourant, 1954, 1983; Greenberg, 1959, 1966; Murdock, 1959; Hieraux, 1975; Nurse et al., 1985; Roychoudhury and Nei, 1988; Howells, 1989). Thus, it is apparent that populations affiliated with the two geographic regions are not closely related to each other.

With this regional differentiation as a baseline, the next step in analysis was to

combine the homogeneous individual samples into the two respective large groups: sub-Saharan and North Africa. This pooling was effected to 1) determine collective regional frequencies, 2) identify the most diagnostic dental traits, and 3) provide a corresponding level of comparison with published data from several large, pooled non-African groups (see below).

The pooled sub-Saharan group ( $n = 976$ ) consists of the original 14 samples, plus Chad, Mesolithic Nubia, and the regional sub-Saharan samples from west, east, and south Africa. The rationale for including

TABLE 3. Comparison of 27 dental crown and root traits in sub-Saharan Africa (SSA), North Africa (NAF), Europe (EUR), Sundadonts (SUN), and Sinodonts (SIN)<sup>1</sup>

Trait <sup>2</sup>	Sample									
	SSA		NAF		EUR		SUN		SIN	
	%	n	%	n	%	n	%	n	%	n
Winging UI1 (+ = ASU 1)	6.6	742	7.4	460	9.0	129	22.8	219	41.4	1,954
Shovel UI1 (+ = ASU 2-6)	28.1	413	19.5	154	17.0	141	79.2	202	98.8	1,922
Double shovel UI1 (+ = ASU 2-6)	1.1	437	8.6	175	23.3	137	14.9	201	71.0	1,781
Tuberculum dentale UI2 (+ = ASU 1-6)	61.2	454	58.7	189	38.1	152	58.1	186	64.2	1,990
Bushman Canine UC (+ = ASU 1-3)	18.1	586	6.1	261	4.8	146	2.0	245	1.2	2,280
Distal accessory ridge UC (+ = ASU 1-5)	71.8	483	34.9	195	51.7	89	65.0	139	73.9	1,073
Hypocone UM2 (+ = ASU 1-5)	99.0	772	95.7	446	79.4	228	92.0	414	90.2	3,639
Cusp 5 UM1 (+ = ASU 1-5)	32.8	619	18.5	357	13.7	212	30.0	370	19.0	2,817
Carabelli's UM1 (+ = ASU 2-7)	51.2	683	54.7	331	47.4	230	30.6	427	32.1	3,194
Parastyle UM3 (+ = ASU 1-5)	2.0	550	1.2	332	4.5	134	1.3	153	4.8	2,400
Enamel Extension UM1 (+ = ASU 1-3)	9.4	574	6.8	503	43.7	286	57.5	388	68.5	5,135
Root no. UP1 (+ = ASU 2+)	58.9	570	57.1	468	34.0	238	40.8	441	12.2	4,757
Root no. UM2 (+ = ASU 3+)	83.7	503	78.6	374	53.8	197	73.9	333	51.8	3,718
Odontome P1-2 (+ = ASU +)	0.4	756	0.2	441	1.2	171	1.4	146	4.6	2,738
Peg-reduced absent UM3 (+ = ASU P, R, C)	5.4	708	18.3	545	20.7	241	44.0	300	22.5	4,623
Lingual cusp LP2 (+ = ASU 2-9)	68.5	530	72.6	270	62.9	159	79.1	278	47.2	2,393
Groove pattern LM2 (+ = ASU Y)	52.4	617	30.6	402	22.9	214	19.6	342	10.9	3,783
Cusp no. LM1 (+ = ASU 6+)	16.6	561	7.7	352	7.9	178	35.5	282	47.8	2,947
Cusp no. LM2 (+ = ASU 4)	24.1	585	66.4	381	65.1	189	40.4	317	7.9	3,583
Deflecting wrinkle LM1 (+ = ASU 1-3)	30.1	432	24.7	267	30.9	149	55.3	161	70.7	1,817
C1-C2 crest LM1 (+ = ASU +)	1.3	447	3.3	276	8.6	185	7.3	96	5.4	2,825
Protostylid LM1 (+ = ASU 1-6)	21.0	556	32.5	351	20.0	200	30.0	337	34.7	3,739
Cusp 7 LM1 (+ = ASU 1-4)	38.5	598	9.4	414	5.8	223	7.4	367	9.8	3,998
Tome's root LP1 (+ = ASU 3-5)	22.4	361	8.6	372	7.4	148	9.8	133	8.2	2,883
Root no. LC (+ = ASU 2+)	0.0	333	2.3	347	4.8	207	0.0	207	0.5	3,722
Root no. LM1 (+ = ASU 3+)	1.7	409	1.2	337	0.8	254	9.3	343	13.8	5,192
Root no. LM2 (+ = ASU 2+)	93.3	388	88.3	333	71.4	224	81.5	297	65.5	4,346

<sup>1,2</sup> Data for SUN (Southeast Asia) and SIN (Northeast Asia and all New World natives) and standard rank-scaled breakpoints from Turner (1985). Data for EUR from Turner (1985) and from Turner's unpublished Poundbury data. All frequencies are of individual counts.

Chad and Mesolithic Nubia with the sub-Saharan Africans involves both dental and numerous other data; it is discussed in detail elsewhere (Irish and Turner, 1990; Irish, 1993, in press) and is not repeated here. The pooled North African group (n = 659) consists of the 12 original samples (excluding Chad and Mesolithic Nubia) and the regional north African sample. Comparison of the two pooled samples on a trait-by-trait basis further supports the evidence for marked interregional divergence; 23 of the total 36 dental trait frequencies differ significantly (refer to Table 5). Trait frequencies from these two samples were then compared to available published data from five non-African groups: Europe, sundadonts, sinodonts, Melanesia, and Australia/Tasmania (Turner, 1985, 1987, 1992a,b).

#### African and Non-African Sample Comparisons

Table 3 lists frequencies of 27 dental traits for the sub-Saharan and North Africans,

plus samples from Europe, Southeast Asia (sundadonts), and Northeast Asia and the New World (sinodonts). Table 4 lists 14 dental traits for the two African samples and Australia/Tasmania and Melanesia. The total 36 traits are not compared because Turner did not report the other features in his respective articles. The African/non-African trait frequencies should be directly comparable to one another because the ASU system was used in all studies, and our interobserver error rate was previously tested and found to be minimum and random (Haeussler et al., 1988; Turner and Irish, 1989). The dichotomized ASU presence/absence breakpoints are listed under each trait's name on the left of the tables. Some breakpoints vary between tables, and this should be considered when comparing trait frequencies.

The North Africans display the strongest similarity to Europeans; both share many features involving dental simplification. Of the 27 traits, only UI1 double shovel, UM1 enamel extension, and UP1 and UM2 root

TABLE 4. Comparison of 14 dental crown and root traits in sub-Saharan Africa (SSA), North Africa (NAF), Australia/Tasmania (AUT), and Melanesia (MEL)<sup>1</sup>

Trait <sup>2</sup>	Sample							
	SSA		NAF		AUT		MEL	
	%	n	%	n	%	n	%	n
Shovel UI1 (+ = ASU 3-6)	5.3	413	3.2	154	15.9	44	9.3	118
Double shovel UI1 (+ = ASU 2-6)	1.1	437	8.6	175	7.0	43	5.0	118
Interruption groove UI2 (+ = ASU +)	13.4	471	36.1	208	21.6	51	18.4	147
Bushman Canine UC (+ = ASU 1-3)	18.1	586	6.1	261	5.0	60	3.2	156
Cusp 5 UM1 (+ = ASU 1-5)	32.8	619	18.5	357	68.2	88	62.4	221
Enamel extension UM1 (+ = ASU 2-3)	0.3	574	3.0	503	8.1	208	4.4	250
Root no. UM2 (+ = ASU 3+)	83.7	503	78.6	374	82.6	178	73.3	240
Peg-reduced absent UM3 (+ = ASU P, R, C)	5.4	708	18.3	545	6.4	220	12.6	270
Cusp no. LM2 (+ = ASU 4)	24.1	585	66.4	381	7.2	97	53.0	219
Deflecting wrinkle LM1 (+ = ASU 3)	2.3	432	0.4	267	17.1	35	17.6	136
Cusp 7 LM1 (+ = ASU 1-4)	38.5	598	9.4	414	8.2	97	11.7	240
Tome's root LP1 (+ = ASU 3-5)	22.4	361	8.6	372	21.6	83	12.1	116
Root no. LM1 (+ = ASU 3+)	1.7	409	1.2	337	5.7	157	3.2	222
Root no. LM2 (+ = ASU 2+)	93.3	388	88.3	333	91.4	152	94.7	209

<sup>1,2</sup> Data for AUT and MEL and standard rank-scaled breakpoints from Turner (1987, 1992a).

number show sizable differences. Mean measure of divergence analysis between the two samples yielded a value of 0.154. North Africans are next most similar to the sub-Saharan sample, suggesting some influence by these peoples; the 27 trait MMD is 0.166. Genetic analyses (e.g., Mourant, 1954, 1983; Hiernaux, 1975; Nurse et al., 1985; Roychoudhury and Nei, 1988) which link North Africans to Europeans yet record many sub-Saharan-influenced traits agree with these findings. North Africans are wholly unlike the sundadonts (MMD = 0.297) and particularly sinodonts (0.671). Based on 14 traits, they are also divergent from the Australian/Tasmanians (0.403) and Melanesians (0.265). In all cases, the MMDs differ significantly (see Sjøvold, 1973, 1977) between samples. These findings are discussed in detail elsewhere (Irish, 1993, in press).

The sub-Saharan Africans are clearly distinct from all other samples (see Table 5), although they bear a slight resemblance to Australia/Tasmania and Melanesia, particularly regarding root traits. For example, chi-square analysis shows that of four such traits only one (LM1 root number) differs significantly between the African and Australian/Tasmanian samples (Table 5). The respective 14 trait MMDs between sub-Saharan Africa and the two South Pacific samples are 0.152 and 0.143 (by comparison, the 14 trait MMD between sub-Saharan and North Africa is 0.216). Turner (1992a) also

noted some dental similarity between sub-Saharan Africa and Australia, and other workers (Giblett, 1969; Nurse et al., 1985; Howells, 1989; Brace and Tracer, 1990) found seeming skeletal and genetic links between the two regions and Melanesia. Cavalli-Sforza et al. (1993) even suggested that after 60,000–55,000 BP, Africans may have developed seagoing skills which allowed them to eventually contact Australia. However, as Turner (1992a:149) states, "the linkage [between Africa and Australia] is neither intuitively satisfying nor supported by any archaeological evidence." And Nurse et al. (1985) suggest that any similarities may involve parallel selection rather than genetic affinity. Recent analyses of several world samples for five blood group loci (ABO, MNSs, Rh, Gm, HLA) may support this view (see Sanchez-Mazas et al., 1986; Roychoudhury and Nei, 1988).

The sub-Saharan Africans are least like sinodonts (MMD = 0.610), despite the fact that both groups have morphologically complex, mass-additive teeth relative to other world populations. Indeed, the two appear to be at opposite ends of a dental morphological spectrum for many traits. Based on the data at hand (Table 3), sub-Saharan Africans exhibit the highest frequencies of Bushman Canine, two-rooted UP1, three-rooted UM2, LM2 Y-groove, LP1 Tome's root, two-rooted LM2, and M3 presence. The sinodonts have the lowest or second lowest frequencies for



TABLE 5. Significant chi-square *P* values (1 df,  $\leq .05$ )<sup>1</sup> for dental traits between sub-Saharan Africa and six other world samples<sup>2</sup>

Sub-Saharan Africa compared with	NAF	EUR	SUN	SIN	AUT	MEL
Winging UI1			.00	.00	— <sup>4</sup>	— <sup>4</sup>
Labial curvature UI1	.00	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>
Palatine torus	.00	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>
Shovel UI1	.03	.01	.00	.00	.02	
Double shovel UI1	.00	.00	.00	.00	.03	.02
Interruption groove UI2	.00	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>		
Tuberculum dentale UI2		.00			— <sup>4</sup>	— <sup>4</sup>
Bushman Canine UC	.00	.00	.00	.00	.01	.00
Distal Accessory Ridge UC	.00	.00			— <sup>4</sup>	— <sup>4</sup>
Hypocone UM2		.00	.00	.00	— <sup>4</sup>	— <sup>4</sup>
Cusp 5 UM1	.00	.00		.00	.00	.00
Carabelli UM1			.00	.00	— <sup>4</sup>	— <sup>4</sup>
Parastyle UM3				.04	— <sup>4</sup>	— <sup>4</sup>
Enamel Extension UM1	.05	.00	.00	.00	.00	.00
Root no. UP1		.00	.00	.00	— <sup>4</sup>	— <sup>4</sup>
Root no. UM2		.00	.00	.00		.00
Peg-reduced UI2	.00	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>
Odontome P1-2				.00	— <sup>4</sup>	— <sup>4</sup>
Peg-reduced absent UM3	.00	.00	.00	.00		.00
Midline Diastema UI1	.00	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>
Lingual cusp LP2			.00	.00	— <sup>4</sup>	— <sup>4</sup>
Anterior fovea LM1	.00	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>
Mandibular torus		— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>
Groove pattern LM2	.00	.00	.00	.00	— <sup>4</sup>	— <sup>4</sup>
Rocker jaw	.00	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>
Cusp no. LM1	.00	.00	.00	.00	— <sup>4</sup>	— <sup>4</sup>
Cusp no. LM2	.00	.00	.00	.00	.00	.00
Deflecting wrinkle LM1	.00		.00	.00	.00	.00
C1-C2 crest LM1		.00	.00	.00	— <sup>4</sup>	— <sup>4</sup>
Protostylid LM1	.00		.00	.00	— <sup>4</sup>	— <sup>4</sup>
Cusp 7 LM1	.00	.00	.00	.00	.00	.00
Tome's root LP1	.00	.00	.00	.00		.01
Root no. LC	.00	.00	— <sup>3</sup>		— <sup>4</sup>	— <sup>4</sup>
Root no. LM1			.00	.00	.02	
Root no. LM2	.00	.00	.00	.00		
Torsomolar LM3		— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>	— <sup>4</sup>
Total significance	23/36	19/27	21/26	24/27	9/14	10/14
Percent significance	64%	70%	81%	89%	64%	71%

<sup>1</sup> Yates correction factor used on cells with expected frequency <5.<sup>2</sup> NAF, North Africa; EUR, Europe; SUN, Sundadontes; SIN, Sinodonts; AUT, Australia/Tasmania; MEL, Melanesia.<sup>3</sup> Chi-square statistic not calculated: two cells = 0.<sup>4</sup> Trait not evaluated.

these same traits. Conversely, the sub-Saharan Africans have the lowest or among the lowest frequencies of such complex traits as UI1 winging, UI1 double shovel, UM1 enamel extension, premolar odontomes, LM1 deflecting wrinkle, and three-rooted LM1; sinodonts have the highest frequencies. In total, 24 of the 27 traits differ significantly between samples (Table 5).

Lastly, with few exceptions (e.g., Europe for UM2 hypocone, four-cusped LM2, two-rooted LC), the 27 North African, European, and sundadont trait frequencies are intermediate to those of extreme sub-Saharan Africans and sinodonts (see Table 3). Those groups which are geographically closer to one another display greater dental similar-

ity and vice versa. For example, disparate sub-Saharan and sinodont samples are farthest apart geographically, a relationship pointed out by Turner (1992b). Conversely, those samples which are closer to sub-Saharan Africa are more dentally similar to the latter group. To illustrate, 27 trait MMD values between sub-Saharan Africa and sundadonts, Europeans, and North Africans are 0.279, 0.244, and 0.166, respectively. The percent of significantly different dental traits (Table 5) decreases in a similar fashion. Thus, these relationships may identify an expansive dental morphological cline that stretches from Sub-Saharan Africa through North Africa into Europe, Southeast Asia, and Northeast Asia and the New World.

This finding, based on morphological data, supports a similar conclusion by Cavalli-Sforza et al. (1993) and others using gene frequencies.

### Sub-Saharan African dental complex

Based on this initial seven sample dental comparison and following the approach of such dental researchers as Hanihara (1967, 1969), Zubov (1979), and Turner (1984, 1985, 1990), I propose that a tentative sub-Saharan African dental complex (the suite of traits that best differentiates these folk from other world populations) consists of a recurrent combination of two low- and nine high-frequency traits (see below). A few of these traits are present in comparable frequencies elsewhere (e.g., North Africa and Europe for UM1 Carabelli's; Australia/Tasmania and Melanesia for LM2 root number), but the prevalence of most differs significantly relative to other world groups (Table 5). Thus, it is felt that the relevant combination of all 11 traits clearly denotes a sub-Saharan pattern.

The complex includes the world's lowest and second lowest frequencies of UI1 double shoveling (1.1%, with a range of 0–8.3%) and UM1 enamel extension (9% at grades 1–3, range 0–27%; 0.3% at grades 2–3) and the world's highest or second highest frequencies of M3 presence (95%, range 86–100%), two-rooted LM2 (93%, 71–100%), three-rooted UM2 (84%, 73–95%), LM2 Y-pattern (52%, 30–83%), UM1 Carabelli's trait (51%, 19–69%), two-rooted UP1 (41%, 20–69%), LM1 cusp 7 (39%, 0–46%), LP1 Tome's root (22%, 0–50%), and Bushman Canine (18%, 0–41%) (Irish, 1993, 1994). Although the latter three traits may not be expressed in all individual sub-Saharan samples (specifically, one sample per trait—Nguni, San, and Congo), these exceptions involve small sample sizes which are apparently not representative of the larger populations. These traits are ubiquitous in all remaining sub-Saharan samples. For example, the lack of Bushman Canine in the Congo sample (0 of 7 canines in 12 individuals) is counter to neighboring groups that are otherwise indistinguishable dentally: Pygmy (MMD = .022), Gabon (.000), Nigeria-Cameroon (.000), and Togo-Benin (.020) (see Fig. 1). The latter

four samples express the trait 20%, 6%, 22%, and 35% of the time, respectively (Irish, 1993). There are analogous examples concerning the absence of LP1 Tome's root in the San and LM1 cusp 7 in the Nguni.

Interestingly, the complex's nine high-frequency traits are also common in the dentitions of various extinct hominids and extinct and extant nonhuman primates (see, among others, Gregory, 1922; Gregory and Hellman, 1926; Weidenreich, 1937; Dahlberg, 1945, 1947, 1968; Robinson, 1956; Le Gros Clark, 1960; Swindler, 1976, personal communication; Wood and Abbott, 1983; Wood et al., 1983, 1988; Hillson, 1986; Wood and Engleman, 1988; Aiello and Dean, 1990; Tobias, 1991; Turner and Hawkey, 1991; Turner, 1992a; Brown and Walker, 1993; Stringer, personal communication; Irish, personal observation). Potential ramifications regarding the ubiquity of these apparent ancestral features in modern sub-Saharan populations, along with the evidence for a dental cline extending out of sub-Saharan Africa, will be explored in a future investigation.

Finally, sub-Saharan Africans also have notable frequencies of UI1 labial curvature (56%, 17–75%) and UI1 midline diastema (13%, 3–44%). Unfortunately, these features are not routinely recorded in other dental studies, so an African/non-African comparison cannot be attempted to determine if they too represent diagnostic African traits.

### CONCLUSIONS

In summary, this investigation provides some new insight into the phenetic relationships of African populations based on dental morphological data. Striking sub-Saharan and North African intraregion homogeneity contrasts with significant interregional differences. And from a global perspective, North Africans resemble Europeans to some degree, whereas sub-Saharan-affiliated Africans differ from all world groups, with only superficial similarity to Australian/Tasmanians and perhaps Melanesians. Sub-Saharan Africans are particularly distinctive in their expression of numerous, morphologically complex dental crown and root traits that are generally absent or found in low frequencies elsewhere. Based on the avail-

able data, I believe this suite of traits is distinctive enough to tentatively designate a separate classification relative to other world dental patterns: the sub-Saharan African dental complex. Indeed, this complex is no less evident than the well-accepted Mongoloid dental complex of Hanihara (1967, 1969), the eastern and western dental complexes of Zubov (1979), and the sinodont and sundadont patterns of Turner (1984, 1985, 1990).

Future analyses will benefit by the examination of additional world samples, particularly if they are subjected to a more specific level of inquiry. Said another way, the same type of investigation as that applied to the individual African samples or to individual Asian and New World samples (see Turner, 1984, 1985, 1987, 1990) will provide much greater detail concerning potential African/non-African relationships. Comparing large pooled samples, as necessitated by the published data, provides an initial idea of worldwide biological affiliation, but the use of many smaller, regional samples will allow finer resolution. Such an approach should also provide additional evidence to test the credibility of the dental complex proposed to characterize African populations south of the Sahara.

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